

**EGG MORTALITY IN THE EASTERN TENT CATERPILLAR,
MALACOSOMA AMERICANUM (LEPIDOPTERA:
LASIOCAMPIDAE): THE ROLE OF ACCESSORY
GLAND SECRETIONS AND EGG MASS SHAPE**

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Abstract.—Four species of hymenopteran parasitoids were reared from egg masses of the eastern tent caterpillar, *Malacosoma americanum* (F.) (Lepidoptera: Lasiocampidae) in New York State: *Telenomus clisiocampae* Riley (Scelionidae), *Tetrastichus malacosomae* Girault (Eulophidae), *Ooencyrtus clisiocampae* (Ashmead) (Encyrtidae), and *Aberus clisiocampae* (Ashmead) (Aphelinidae). Three classes of host eggs were distinguished, exposed eggs, eggs covered with spumaline on the margin of the mass, and eggs covered with spumaline in the interior portion of the mass. Parasitism rates of exposed (27%) and covered marginal eggs (23%) were significantly greater than covered interior eggs (1%). Inviability was greater in exposed and covered marginal eggs relative to interior eggs. An analysis of relationships within *Malacosoma* indicates that frothy spumaline is an evolutionarily labile trait and has undergone either multiple elaborations or parallel reductions. The hypothesis that frothy spumaline has evolved convergently in *Malacosoma* species as a response to hymenopteran egg parasitoids is discussed.

Egg parasitoids (primarily of the hymenopteran superfamilies Chalcidoidea and Proctotrupeoidea) are one of the most important biological factors affecting the survival of many species of Lepidoptera and Hemiptera. Their influence is not as widely appreciated as that of larval, nymphal, and pupal parasitoids, in large part because of the difficulty in sampling egg populations. Where data are available, commonly more than 50% of the eggs are parasitized (Anderson, 1976). Such high rates indicate strong selective pressures on the host to reduce loss, for example, by elimination of the cues used by parasitoids to locate the eggs, or to provide the eggs with a means of protection if they are found.

The oviposition behavior of species in the genus *Malacosoma* Hübner

(Lepidoptera: Lasiocampidae) is particularly interesting with regard to egg parasitism. The European pest species *M. neustria* (L.) is typical of all Old World species of the genus. It lays its eggs in a single-layered exposed mass on twigs; a typical mass contains 140–200 eggs (Schwenke, 1978). In these masses parasitism rates of 40% have been recorded (Romanova and Lozinskij, 1958).

In contrast parasitism rates in New World *Malacosoma* have never been found to exceed 15% and are usually much lower (Anderson, 1976; Witter and Kulman, 1972). All New World species except *M. tigris* (Dyar) cover their egg masses with a foamy, accessory gland secretion known as spumaline. Hodson (1939) noted that egg parasitism of *M. disstria* Hübner is concentrated in eggs along the margin of the mass and suggested that this was due to the incomplete covering of spumaline in this area. Other authors have anecdotally referred to prevention of parasitism as the function of spumaline (e.g. Stehr and Cook, 1968; Wellington, 1965; Witter and Kulman, 1979). Prentice (1953) reported that *M. disstria* eggs covered with spumaline were less heavily parasitized (2.3%) than those exposed (60.9% in partially covered masses; 72.5% in completely exposed masses). He cited only these percentages and gave none of the information necessary to evaluate his conclusion (e.g., sample size, variation). The function of spumaline therefore merits further investigation.

In this paper we present natural history information on the egg parasitoids associated with *Malacosoma americanum* (F.). We compare parasitism and inviability rates of eggs as functions of both position within the mass and spumaline covering. We discuss the possible role of egg parasitoids in the evolution of oviposition behavior in the genus *Malacosoma*.

METHODS AND MATERIALS

Egg masses of *Malacosoma americanum* were collected in the spring of 1980 prior to the hatching of caterpillars. A total of 90 egg masses were collected from four localities in central and western New York State (Ithaca, Beebe Lake, Tompkins Co., $n = 17$ egg masses; Ithaca, Cascadilla Creek, Tompkins Co., $n = 30$; Texas Hollow Wildflower Preserve, Schuyler Co., $n = 28$; and Dunkirk, Chautauqua Co., $n = 15$). Egg masses were then scored as either completely covered with spumaline or as having some exposed eggs. All exposed eggs were marked with paint to allow recognition after caterpillar emergence.

Egg masses were maintained at 21°C, 63% relative humidity, and 12/12 hour photoperiod until after the hatching of caterpillars and parasitoids. Unhatched eggs were then examined to determine both parasitism and inviability rates.

Data collected from each parasitized egg consisted of identity of parasitoid, date of emergence, position in the egg mass, and whether or not it was

Table 1. Composition of egg parasite fauna on *Malacosoma americanum* from 4 localities in New York. [% composition and (number of individuals). Total: 937 parasitoids.]

Locality (n = egg masses)	<i>Tetrastichus malacosomae</i>	<i>Telenomus clisiocampae</i>	<i>Ooencyrtus clisiocampae</i>	<i>Ablerus clisiocampae</i>
Dunkirk (n = 13)	.541 (92)	.159 (27)	.294 (50)	.006 (1)
Beebe Lake (n = 15)	.900 (226)	.068 (17)	.028 (7)	.004 (1)
Cascadilla Ck. (n = 26)	.761 (124)	.147 (24)	.080 (13)	.012 (2)
Texas Hollow (n = 22)	.926 (327)	.065 (23)	.008 (3)	—
Totals	.821 (769)	.097 (91)	.078 (73)	.004 (4)

covered with spumaline. Four species of hymenopteran egg parasitoids were encountered in this study: *Ablerus clisiocampae* (Ashmead) (Aphelinidae) which appeared first, followed, in order of emergence, by *Telenomus clisiocampae* Riley (Scelionidae), *Ooencyrtus clisiocampae* (Ashmead) (Encyrtidae), and *Tetrastichus malacosomae* Girault (Eulophidae). Vouchers of specimens are deposited in the Cornell University Insect Collection, lot no. 1107. Locations of parasitized host eggs in the mass were scored as exposed, not covered with a layer of frothy spumaline; covered marginal, on the perimeter of the egg mass or next to an exposed egg; or covered interior, and ranked according to the number of eggs by which it was separated from the margin. Another source of egg mortality was the failure to produce either a caterpillar or a parasitoid wasp. These were termed inviable eggs, and their positions within the egg mass were also recorded. Ten egg masses were then randomly chosen for a detailed analysis of parasitism rate, inviability rate, and the distribution of parasitized eggs in the egg mass.

A weakness in previous studies on egg parasitoids has been the failure to separate eggs that do not hatch from those that produce parasitoids. Previous investigators simply counted and identified the parasitoids and estimated the size of the egg mass (e.g. Hodson, 1941; Romanova and Lozinskij, 1958). This procedure does not allow assessment of the relative contributions of parasitism and inviability to mortality.

Our procedure determined the fate of each egg along with its position and the distribution of spumaline on the egg mass. Parasitoid identity was established by the distinctive shape and color of the meconium of each species. *Telenomus clisiocampae* produces a yellowish-green amorphous meconium; *Tetrastichus malacosomae* deposits large dark green, ovoid pel-

Table 2. Distribution of parasitized and inviable eggs in ten egg masses of *M. americanum*. (Exp = exposed eggs; Marg = marginal eggs; Int = interior eggs; as defined in text.)

Egg Mass	No. Egg	No. Exp	No. Marg	No. Int	Parasitism Rate			Inviability Rate		
					Exp	Marg	Int	Exp	Marg	Int
cc19	145	3	43	99	0	.209	0	.33	0	0
cc18	339	2	65	272	0	.123	.004	.500	.062	.004
cc12	387	3	39	345	.333	.462	.020	.667	.077	.009
cc11	290	18	77	195	0	.169	0	.278	.208	.031
cc4	120	3	43	74	0	0	0	0	.046	.027
th29	272	31	81	160	.452	.272	0	.258	.062	0
th21	339	36	56	247	.361	.232	.012	.056	.089	.004
th9	216	18	45	153	.333	.333	0	.167	.044	.007
th8	203	8	51	144	.750	.275	.062	.250	.137	.076
bl12	274	4	64	206	.500	.172	.005	0	0	0
Mean	258.5	12.6	56.4	189.5	.272	.225	.010	.251	.073	.016
SD	86.82	12.6	14.8	81.9	.263	.125	.019	.214	.062	.024

lets; *Ooencyrtus clisiocampae* and *Alerus clisiocampae* both produce small black pellets. The latter two species were distinguishable because their emergence periods did not overlap. Successful development of the caterpillar was determined by a completely empty opened egg (chorion), with neither yolk nor meconium, or by the presence of the caterpillar within unhatched eggs. The ten egg masses contained at least one viable exposed egg. We used *t*-tests to compare the mean differences in parasitism and inviability rates in the ten egg masses for all three pairwise combinations of egg location (exposed versus interior, exposed versus marginal, marginal versus interior).

RESULTS

Malacosoma americanum populations have been relatively large in the study sites in the three years preceding this study (1976–1979), and a high proportion of the egg masses were parasitized (89%). Interlocality variation in the proportion of masses parasitized varied from 100% at Texas Hollow to 76% at Cascadilla Creek. Exposed eggs occurred in 64% of the 76 egg masses, with the number of exposed eggs usually quite low (mean = 13, SD = 10).

Table 1 documents the composition of the egg parasitoid fauna of *M. americanum* in the four upstate New York localities; *Tetrastichus* is clearly the most abundant egg parasitoid. The same rank order of these four parasitoids was found in a study conducted in Ithaca, New York, in 1924 (Liu, 1926), but in that study *Telenomus* was a much more important mortality

Table 3. Comparison of the distribution of the 3 most common species of parasitoids within egg masses of *M. americanum*. The χ^2 values test the null hypothesis of equal numbers of parasitoids in marginal and interior eggs classes. Note that the number of eggs in the two classes are not equal (Table 2). [% of occurrences, (number of individuals).]

Species	Marginal Eggs	Interior Eggs	χ^2
<i>Tetrastichus malacosomae</i>	.730 (492)	.270 (182)	75.27 ^a
<i>Telenomus clisiocampae</i>	.518 (56)	.482 (52)	.074 n.s.
<i>Ooencyrtus clisiocampae</i>	.427 (32)	.573 (43)	.811 n.s.

^a Significant at $P = .001$; n.s.: $P > .25$.

factor (30% of reared wasps versus 10%). Parasitoid abundance varies on a regional basis; parasitism by *Ooencyrtus* ranged over an order of magnitude in this study alone.

Table 2 summarizes the results of the detailed analysis of ten egg masses. Parasitism rates are significantly higher in exposed than interior eggs ($t = 4.69$, 9 *df*, $P < .001$), and significantly higher in marginal than interior eggs ($t = 8.02$, 9 *df*, $P < .0005$). Exposed and marginal eggs do not differ significantly in parasitism rate ($t = .950$, 9 *df*, $P > .10$).

Inviability rates were significantly higher in exposed than marginal eggs ($t = 3.75$, 9 *df*, $P < .01$), higher in marginal than interior eggs ($t = 4.94$, 9 *df*, $P < .0005$) and higher in exposed than interior eggs ($t = 4.84$, 9 *df*, $P < .0005$).

The distribution of the three most common species of parasitoid within the egg mass was also compared ($n = 90$ egg masses). Table 3 summarizes the results. *Telenomus* and *Ooencyrtus* were equally common in the interior and marginal egg classes. *Tetrastichus* is more closely associated with the egg mass margin (73%) and this distribution is significantly different from that of both *Ooencyrtus* ($\chi^2 = 28.9$, $P < .001$) and *Telenomus* ($\chi^2 = 20.0$, $P < .001$).

DISCUSSION

In *Malacosoma americanum* egg survival is strongly correlated with the relative position in the egg mass and with the covering of frothy spumaline. Exposed eggs, i.e. those without a spumaline covering, average 27% parasitism and 25% inviability rates. The most vulnerable position within the covered portion of the egg mass is along its perimeter (23% parasitism, 7% inviability). The same general trends appear to be true for *M. disstria*. Clearly, the best oviposition strategy for a female of *Malacosoma* is to cover all eggs with spumaline and to minimize the number of marginal eggs in the mass.

The number of marginal eggs can be changed by altering the shape of the

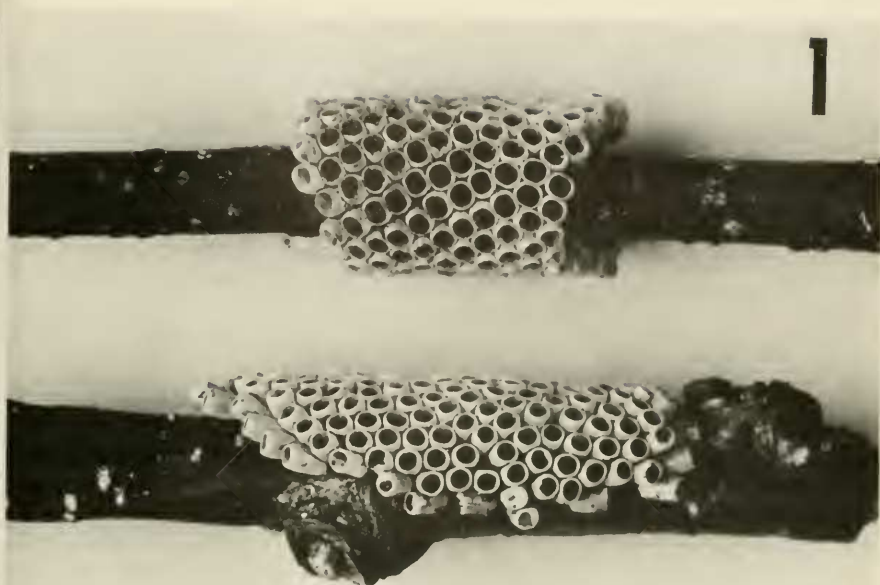


Fig. 1. Egg masses of *M. americanum* (bottom) and *M. distria* (top). *M. americanum* has a clasp egg mass; *M. distria* has a helical egg mass. Note the deviation of the marginal eggs of *M. americanum* from the vertical orientation.

egg mass. Two general egg mass shapes are found in *Malacosoma*, clasp (found in *americanum*, *californicum* (Packard), and *incurvum* (Hy. Edwards) and helical (all other species). These terms refer to the final shape of the mass and are a result of differences in oviposition behavior. According to Stehr and Cook (1968), in all species the female oviposits with the longitudinal axis of the body perpendicular to the twig. She swings her abdomen from side to side, laying eggs in a single row, and then moves forward and around the twig. The difference in shape between the two kinds of masses results from varying numbers of eggs laid in each row. Those species forming a helical mass lay only three to four eggs before moving around the twig. The female completely circles the twig several times and packs the eggs as tightly together as possible. The resulting egg mass is roughly cylindrical. The clasp species lay a row of ten to fifteen eggs. As the female oviposits she moves around the twig, but generally does not move far along its longitudinal axis. The egg mass is usually saddle-shaped, occasionally completely encircling the twig and sometimes even overlapping upon itself (Fig. 1).

The type of egg mass will determine the proportion of eggs placed in the vulnerable marginal row. Assume that the eggs are cubic in shape with unit length (u) for each side and unit area for each face. Assume also that the clasping mass has a circular outline so as to minimize the number of marginal eggs in the egg mass (note, an elliptical egg mass will have an even greater number of marginal eggs). Consider a circular clasping egg mass of 260 eggs (the average for *M. americanum*, see below) laid so that the mass completely encircles the twig, but does not overlap itself. The twig would have a circumference of 18.2 eggs, the diameter of the egg mass ($\pi r^2 = 260u$, $r = 9.097u$, $d = 2r = 18.2u$). This egg mass would have 57 marginal eggs along the circumference of the mass (circumference = $2\pi r = 2\pi 9.09u = 57.7u$), and 22% of the total eggs would be marginal. A helical egg mass laid as a perfect cylinder would have two circles of marginal eggs, one at each end of the egg mass. If laid on the same diameter twig, 18.2u, there would be a total of 36 marginal eggs, with 14% of the total eggs on the margin. Clearly, the optimal egg mass shape, the one minimizing the number of vulnerable marginal eggs, is the helical (cylindrical) egg mass.

Considerations of the phylogeny of *Malacosoma* (see below) indicate that the clasping egg mass is derived (apomorphic) and the helical mass ancestral (plesiomorphic). How can we explain the evolution of this change in oviposition behavior, considering the relatively high marginal mortality rates and assuming the presence of frothy spumaline?

One possibility is that we have overestimated the vulnerability of some of the marginal eggs in clasping egg masses. In those cases in which the lateral edges of the mass are closely approximated and the space between them filled with spumaline, eggs that by our definition are marginal are probably as well protected as interior eggs. If egg masses are laid on very small twigs the clasping egg mass may completely encircle the twig. The last laid row(s) are then laid atop the first laid row(s). In the instances in which we found overlapping eggs, those in the lower layer were rarely parasitized (1%, $n = 76$ eggs). Nevertheless, in the majority of masses the eggs do not encircle the twig (81%, $n = 63$).

We have also observed that the long axes of the marginal eggs of *M. americanum* are usually slanted both away from the perpendicular and away from the center of the mass, sometimes to the extent that the eggs are lying parallel to the twig. This is in contrast to the eggs of *disstria* which are almost always parallel to one another and each perpendicular to the surface of the twig (Fig. 1). This slanting effect increases the distance of the second row of eggs from the edge of the spumaline layer and should result in a lower parasitism rate of the interior eggs. The second and third row parasitism rates cited by Hodson (1939) for *disstria* are indeed greater than those we have found for *americanum* (Fig. 2).

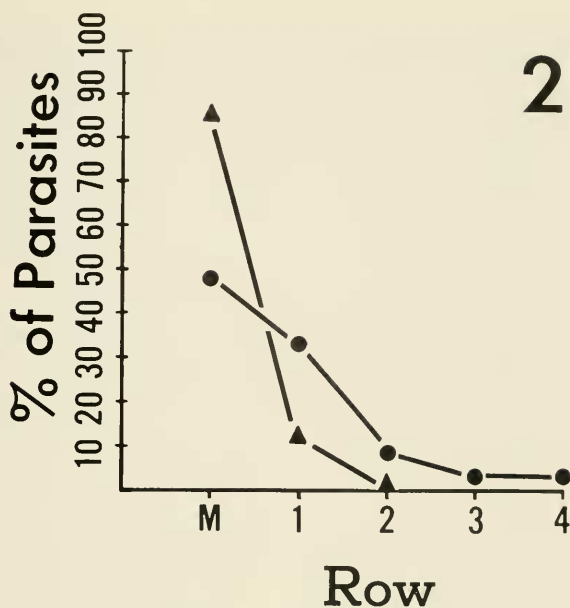


Fig. 2. Distribution of parasites by row. *Malacosoma americanum* (●) [present study, $n = 10$ egg masses] and *M. disstria* (▲) [from Hodson, 1939, $n = 52$ egg masses].

The egg masses of *M. americanum* generally contain many more eggs (mean = 259, SD = 76.8, $n = 13$ egg masses) than those of either *disstria* (mean = 155 eggs; Hodson, 1941) or *neustria* (140–200 eggs; Schwenke, 1978). The clasping mode of oviposition may be necessary if the female is to carry and lay a large number of eggs. A large egg mass, in turn, may be needed to provide a large number of caterpillars, either for the construction of large permanent tents (lacking in *disstria*), or for communal foraging. Finally, a clasping egg mass may enable the female to oviposit on large diameter twigs or even low on tree trunks normally covered by winter snows. The latter is apparently common in the northern Great Lakes region, but is very rare in New York State. A comparison of the low temperature survival rates of pharate larvae of *americanum* and *disstria* may, in fact, provide the key for understanding the evolution of this egg mass shape.

There are interesting differences in the relative abundances of the parasitoid species of *M. americanum* and *disstria*. Species of *Tetrastichus*, *Ooencyrtus*, and *Telenomus* are the most abundant egg parasitoids of both species. In our study of *M. americanum* 80% of the parasitoids were *Tetrastichus malacosomae*, and over 70% of these individuals were reared from marginal eggs (Table 3). In *M. disstria*, parasitism is primarily due to

Ooencyrtus clisiocampae and *Telenomus clisiocampae* which occur in equal numbers and account for 80% of the total parasitism with only 20% mortality due to *Tetrastichus silvaticus* Gahan (Hodson, 1939). In *M. americanum*, *Ooencyrtus clisiocampae* and *Telenomus clisiocampae* show no preference for the marginal egg class (Table 3). The more even distribution of parasitized eggs in *M. disstria* may reflect the relative importance of these two parasitoids. The predominance of *T. malacosomae* in *M. americanum* may be a reflection of the preference for marginal eggs by this species and the greater numbers in this egg class due to the clasping mode of oviposition.

All species of *Malacosoma* deposit a glandular secretion with each egg (Stehr and Cook, 1968). Hodson and Weinman (1945) coined the term "spumaline" to refer to these glandular materials, regardless of the final form. In many species the spumaline is elaborated into a frothy material which covers the eggs, referred to here as frothy spumaline. This type of spumaline is found in all New World species except *M. tigris*.

Two hypotheses have been proposed for the adaptive significance of frothy spumaline: (1) Reduction of egg parasitism (Hodson, 1939) and (2) resistance to desiccation (Hodson and Weinman, 1945). The data of Hodson and Weinman for *M. disstria* agree with ours for *M. americanum*: inviability rates are significantly higher in exposed eggs than those covered with frothy spumaline. However, if spumaline elaboration is primarily a response to desiccation, then one must explain the resistance to desiccation in the arid-land species *M. tigris* and in all Old World species.

The high parasitism rates in exposed eggs (27%) versus internal eggs (1%) suggests that frothy spumaline is a deterrent to egg parasitoids. However, it is not completely effective in eliminating parasitism in eggs along the margin of the mass in either *M. americanum* or *disstria*. This is not a result of a more ragged covering near the margin as was suggested by Hodson (1939). All eggs scored as marginal in our study were completely covered with a frothy spumaline. In both species over 90% of the parasitized eggs were found in the outside two rows. This strongly suggests that the spumaline does not function as a repellent to parasitic Hymenoptera; rather it acts as a physical barrier separating the wasps from potential hosts.

The distribution of frothy spumaline in species of *Malacosoma* can provide ecological insights only in the context of the phylogeny of the genus. The phylogenetic relationships of *Malacosoma* have not been resolved, but Stehr and Cook (1968) present morphological, ecological and behavioral data that establish the following groups as monophyletic (Table 4): *tigris* + *constrictum*, *neustria* + *disstria*, and *americanum* + *incurvum* + *californicum*. The possible relationships among these three groups are illustrated in Fig. 3. Alternative A is suggested by the distribution of character 10, but we prefer to consider the relationships of these three groups as unresolved pending detailed studies. Species with frothy spuma-

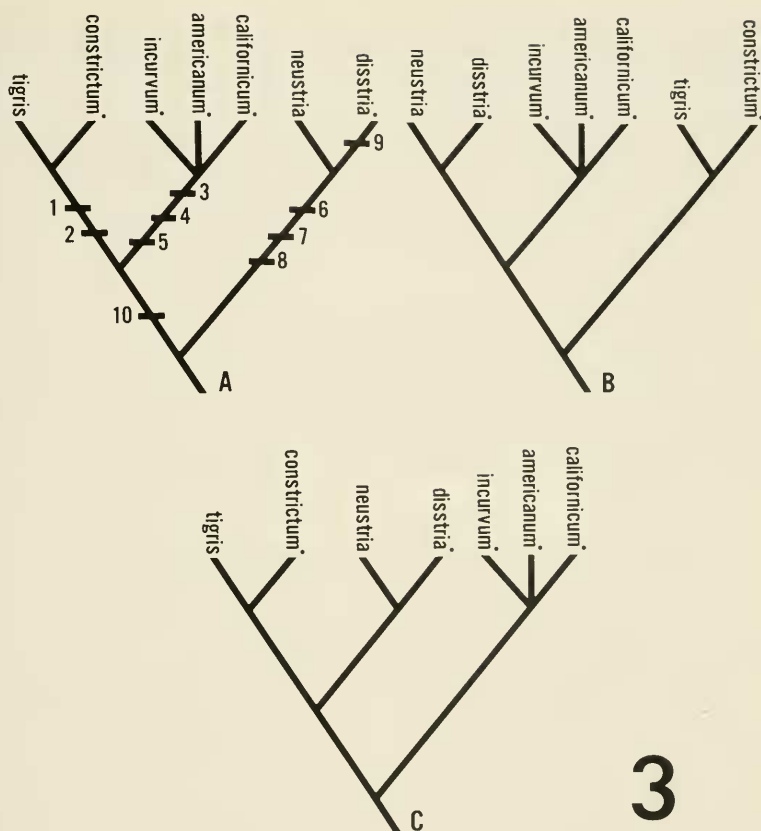


Fig. 3. Three possible cladograms of *Malacosoma* species-groups, with species with a frothy spumaline indicated (*). Numbers refer to characters in Table 4. [See text for discussion.]

line are indicated (*) and appear in each of the three groups. No other members of the genus have frothy spumaline. There are two equally parsimonious interpretations of the pattern of spumaline elaboration for all cladograms in Fig. 3, either frothy spumaline evolved in the common ancestor of all seven species, and was subsequently lost in *neustria* and *tigris*, or frothy spumaline was independently developed three times, in the ancestor of *americanum* + *californicum* + *incurvum*, in *disstria* and in *constrictum*.

Either interpretation establishes that frothy spumaline is an evolutionarily labile character, with either convergences or parallel reductions. We favor the view that a frothy spumaline has evolved independently at least three times for the following reasons:

1. The loss of frothy spumaline in *M. neustria* would result in a substantial

Table 4. Character states of *Malacosoma* species. Polarity determined by considering the European species, *M. franconicum* Esper, *castrensis* (L.), *alpicola* (Staudinger) as the out-group. Data derived from Stehr and Cook, 1968.

Character No.	Ancestral	Derived
1	Large, permanent tents	Small tents, used only during moulting
2	Feed on many plants	Restricted to oaks
3	Helical egg mass	Clasping egg mass
4	Upper posterior corner of ovipositor valves not produced, rounded or angulate in lateral view	Upper posterior corner of ovipositor valves produced as flattened lobes, strongly angled in lateral view
5	Upper posterior corner of ovipositor valve rounded or only slightly produced	Upper posterior corner of ovipositor valve strongly produced
6	Male epiphysis of foreleg small or absent	Male epiphysis large and sickle-shaped
7	Larval setal group L2 with 3 setae	Setal group L2 with 2 setae
8	Larval setal group D1 with 5 setae	Setal group D1 with 4 setae
9	Large, permanent tents	Tent absent
10	Rear margin of male 7th sternum strongly and coarsely serrate	Rear margin of male 7th sternum sinuous, smooth or slightly denticulate

increase in mortality due to parasitism, from the 5–10% loss in species with frothy spumaline (7.0% in this study) to the level of 20–40% observable today (Tadic, 1965; Romanova and Lozinskij, 1958). We can conceive of no selective advantage to the elimination of the spumaline coating that could offset such an increase in egg mortality.

2. The evolution of the clasping egg mass in the *americanum* group presents a dilemma only if frothy spumaline occurred either simultaneously or before the change in egg mass shape. No selective disadvantage due to marginal egg parasitism would obtain in shifting from a helical to the clasping egg mass if spumaline was not present; all eggs are equally vulnerable. For the clasping egg mass to precede spumaline elaboration in the *americanum* group requires that spumaline evolved convergently at least three times.

3. Frothy spumaline requires only a modification of existing accessory gland secretions, primarily by the incorporation of bubbles. It is noteworthy that the accessory glands of *M. tigris*, which has unmodified spumaline, produce as much material as other New World species (Stehr and Cook, 1968).

On the basis of these observations we feel that a frothy spumaline covering was not lost in *neustria* and *tigris*, but was evolved independently in *disstria*, *constrictum* and the *americanum* species group as a mechanism to decrease egg parasitism. Parasitoids have been linked several times to the evolution of parental guarding of eggs by the host species (see, e.g. Eberhard, 1975; Odhiambo, 1959; Ralston, 1977). We expect that further studies on the evolution of mating and oviposition behavior of hosts will continue to demonstrate the influential role played by chalcidoid and proctotrupoid egg parasitoids.

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